Sympatric speciation of freshwater mussels (Bivalvia: Unionoidea): a model

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Abstract: Speciation of freshwater mussels (Bivalvia: Unionoidea) can occur sympatrically (ecologically) via new glochidial host acquisition. Due to the characteristics of the unionoidean life cycle, this hypothesis overcomes the objections of the classical allopatric speciation paradigm, namely homogamy and linkage of mate and habitat preferences. Examples of freshwater mussel populations in various stages of the speciation process are provided from the literature.

Key words: Unionoidea, host race, parasitism, sympatric speciation, speciation model

Inclusion of a parasitic stage in the life cycle of a taxon influences the nature and rate of its speciation. Parasitic taxa can diverge in allopatry when peripheral populations of parasite and host co-evolve subsequent to isolation from their respective parent stocks (Mayr, 1970). Another mechanism of population subdivision available to parasitic species is the formation of host races. Although confusion exists regarding the meaning of the term "host race" (see Mayr, 1970), Bush (1974:3) defined it to describe "... an infraspecific category generally applied to populations of a parasitic species which exhibit distinct genetically-based preferences [for certain hosts]." The concept of host race formation has not, in the strict sense, been applied to freshwater mussels (Bivalvia: Unionoidea).

The impact of their glochidial hosts on the population structure of mussel species has been noted in the literature as far back as Ortmann (1920). Kat (1983; also Kat and Davis, 1984), for example, determined that unionoideans that utilized anadromous hosts maintained a high degree of genetic similarity between widely separated demes, while subpopulations of mussels that infested territorial fish diverged more rapidly. Because the population structure of freshwater mussels is so dependent on the ecology of their hosts, Kat (1984) also suggested that an intraspecific change in host fish might precede the formation of new species. Kat cited Bush's (1974) model of fruit fly speciation via host race formation as relevant to the Unionoidea, and I propose here to extend these ideas, in particular, their applicability to the concept of speciation without geographic isolation.

THE LIFE CYCLE OF FRESHWATER MUSSELS

Although the mechanics of the unionoidean life cycle have been sufficiently detailed elsewhere (*e. g.* Coker *et al.*, 1921; Kat, 1984), the biological implications of the various stages of this process have been largely ignored. To this end, an overview of mussel reproduction follows to emphasize certain points bearing upon the speciation model. The life cycle is here divided into four stages: spawning, brooding, encystment and dispersal, and adulthood.

Spawning

Male mussels expel their sperm directly to the water, and these are eventually entrained in the respiratory current of the female. Work with sea urchins (Pennington, 1985) has shown that even under low flow conditions, sperm diffuse rapidly, and the probability of fertilization decreases to nearly zero for females only a meter downstream. Unfortunately, such work has not been done for freshwater bivalves, but it is reasonable to expect a similar spatial-probability picture (Downing *et al.*, 1993). The range of fertilization, though, could be slightly increased by

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the mussels' greater ability to filter the water column and by the way they package their sperm (D. Ó Foighil, pers. comm.). Freshwater mussels, like oysters, possess spermatozeugmata (Edgar, 1965; Lynn, 1994) which deliver many sperm together rather than let them freely diffuse and be lost (see Ó Foighil, 1989).

Brooding

Mussel embryos develop into larvae, known as glochidia, within the female's ctenidial marsupia. With maturity and appropriate environmental conditions, the glochidia are shed into the water. The extrinsic stimuli leading to glochidial release vary from seasonal fluctuations in temperature and food availability (as in *Margaritifera* spp.; Ziuganov *et al.*, 1994) to the presence of a potential host (as in *Lampsilis* spp.; Kraemer, 1970). There is intra- and interspecific variability in the timing of spawning, length of the brood period, and the time of glochidial release (*e. g.* Zale and Neves, 1982; Neves and Widlak, 1988).

Encystment and Dispersal

Glochidia undergo metamorphosis while encysted in the gill or fin epithelium of an appropriate fish (or, in one case, amphibian) host. Glochidia, incapable of selecting a suitable fish, reach their hosts passively and clamp to any tissue they contact (Lefevre and Curtis, 1910). Certain species, especially those of the genus *Lampsilis*, exhibit behaviors and morphologies capable of attracting fishes (Kat, 1984), increasing the probability of glochidia contacting a potential host. However, the actual specificity of attraction by mantle flaps and conglutinates has yet to be determined. After encysting to a potential host, those glochidia that do not evoke an immune response from the fish are able to complete their metamorphosis (Bauer and Vogel, 1987).

During encystment (lasting days to months), the glochidia are dispersed by the fish to new sites. Adult mussels are capable of limited movement, but the distances traveled are generally short (Amyot and Downing, 1997) and the progress is erratic (figured in Baker, 1928, and Mathiak, 1979); significant dispersal is facilitated only by their hosts. Because the habitat of an adult mussel is a function of where it excysted (Isley, 1911, 1914), it is expected to be found in the habitat preferred by its host. Mussels themselves have low habitat specificity (Strayer, 1981; Strayer and Ralley, 1993) and possess a plastic phenotype (*e. g.* Ortmann's Law of Stream Distribution; Ortmann, 1920) enabling their adaptability to various stream conditions (Watters, 1994b).

THE MODEL

Some model elements are common to all Unionoidea, such as limited fertilization range and conformation to the host habitat. Other factors which might not apply to all mussel species need to be evoked for the model presented here.

The model mussel population has high host specificity. Initially, this specificity is limited to one or possibly a few of the fish species present over the range of the mussel population. Although certain mussel species are characterized by low host specificity, other unionoideans do possess this type of high specificity (Hoggarth, 1992; Watters, 1994a).

Host specificity is under genetic control, and through spontaneous mutation the mussel population has developed the ability to parasitize a new host. The basis of host specificity is immunological (Bauer and Vogel, 1987). If the immune defenses of the infested fish recognize the surficial molecules of the glochidium as foreign, the parasite will be sloughed off. Such glochidial molecules must be under genetic control. That the host specificity of a particular mussel is under genetic control is also evidenced by the fact that mussels sharing a gene pool (*i. e.* species) tend to share host species.

Congeners often employ different host species (Hoggarth, 1992). During the course of their divergence from the ancestral population, additional hosts must have been added to the repertoire of these species. The mechanism by which this new host is added to the population need not necessarily be mutation; any of the normal processes that increase the genetic diversity of a breeding population (*i. e.* recombination, hybridization, etc.) are also acceptable.

The original fish host and the new host have different habitat requirements, and these fish have a strong preference for these habitats. For example, one host prefers riffles, while the other prefers pools; or one might prefer lakes and the other rivers. This can most often be achieved when the new and old hosts belong to different genera. The fish are not ecologically excluded from moving through habitats other than their preferred one.

The two fish hosts differ in their seasonal presence over the range of the mussel population. For instance, one host might be more prevalent late in the mussels' breeding season while the other fish might occur in greater numbers early in the breeding season.

The timing of glochidial release is heritable; it is ultimately under genetic control and can be acted upon by selection. Glochidial release (and spawning) can be triggered by an array of environmental cues such as day length, water temperature, and perhaps host presence. However, the basis for the mussels' perception and recognition of these cues is doubtless the result of physiological characters encoded in the mollusks' genome. Different mussel species exhibit different characteristic breeding periods

(Watters, 1994a), and one reasonable explanation is that the timing of glochidial release is under genetic control.

Due to high host specificity and the population's dependence on the fish for dispersal, the mussels are initially distributed over the habitat of the original host. If the original host spends 90% of its time in its preferred habitat, then about 90% of the mussel population should also occur there.

If the new host occurs, even infrequently, in the habitat of the mussels during their breeding period, these fish could serve as the host for mussels that possess the mutant phenotype (*i. e.* those able to parasitize the new host). Such mussels will begin slowly to accumulate (over many generations) in the new host's habitat, and the result will be at least partial habitat separation of the two phenotypes.

Because of the limited range of fertilization (see above), the tendency would be for adjacent mussels (*i. e.* within the same habitat) to interbreed. Thus, host specificity not only biases the habitat in which a mussel lives but also the phenotype of its mates. *Mussels with a particular host specificity will mate more frequently with mussels sharing the same specificity (homogamy) because of their proximity.* Linkage of mate and habitat "preferences" is the primary assumption of theories proposing reproductive isolation without geographical separation (Maynard Smith, 1966), but it is also a major bone of contention of the classic allopatric-geographic speciation paradigm (Mayr, 1947).

Temporal differences between the presence of the two fishes would contribute selection pressure towards the isolation of the two mussel phenotypes. Those mussels whose glochidial release coincides with peak host availability will have an obvious advantage over those that release their glochidia at other times; this would lead to synchronization of glochidial release with host presence. Kat (1984) has suggested that synchronization of mussel reproduction and fish activity is among the least specialized adaptations that unionoideans have evolved to increase the probability of glochidia encountering an appropriate host.

Fig. 1 shows an overview of the speciation model. At Stage A, the mussel population is distributed over the habitat range of the original host. New individuals are added to the population and tend to remain in the fish's preferred habitat. Between Stages A and B, a mutation appears that allows some members of the population to infect the new host. During Stage B, the mussels possessing the mutant phenotype accumulate in the habitat of the new host. Stage B can last many generations as the number of glochidia produced each generation that survive to reproductive age is very small.

Successful mating can occur in the new habitat after the mussels have accumulated to the point that their density

is conducive to fertilization (Downing *et al.*, 1993); this marks the beginning of Stage C. Interbreeding occurs within but not between the habitats and there is a tendency for glochidia produced to remain in the habitat in which they were conceived. Thus, gene flow between the habitats is limited.

Over time, selection synchronizes the breeding of these two phenotypes with the habits of their respective host fish. This further decreases the amount of gene flow between the two incipient host races. Selection can accelerate this process by contributing to the spawning asynchrony of the two host races. Eventually, Stage D is reached when the two breeding types have become completely isolated due to their opposite host and habitat affinities.

The biological basis for the mutation in host specificity is immunological. It might also be reasonable, however, that the initial change in host specificity is due to a mutation that changes the time of glochidial release, with the habitat preferences of the host contributing selection towards separation. Conceptually, this would require a minor modification of the assumptions, but the same model remains applicable.

EXAMPLES

There are no unequivocal examples in the literature. Finding examples of populations in the early stages of this type of speciation process has proven especially difficult; a simultaneous examination of a mussel population's genetics and host preferences has yet to be undertaken. Provided for illustration are two unionoidean populations that could be candidates for just such a future study.

The first example involves *Anodonta woodiana* (Lea, 1834) in Japan. The "population" is composed of genetically and morphologically distinguishable sympatric morphs (A and B) (Tabe *et al.*, 1994). Further distinguishing these mussels is their breeding period. Morph A is tachytictic and releases its glochidia in late spring and early summer, while Morph B mussels are bradytictic with glochidial release occurring in the early spring (Fukuhara *et al.*, 1994). The reported fish hosts for *A. woodiana* are a goby and at least one cyprinid, and it has been shown that different hosts of this species are associated with different periods of mussel gravidity (Watters, 1994a).

Elliptio waccamawensis (Lea, 1863), a second example, is endemic to Lake Waccamaw and the Waccamaw River of the Atlantic Slope drainage of North Carolina (Johnson, 1970). Electrophoretic studies of members of the genus *Elliptio* indicate that this mussel is most closely related to *Elliptio cistelliformis* (Lea, 1863), which is also found in the lake as well as surrounding drainages (Davis *et al.*, 1981). Davis and co-workers (1981) reported
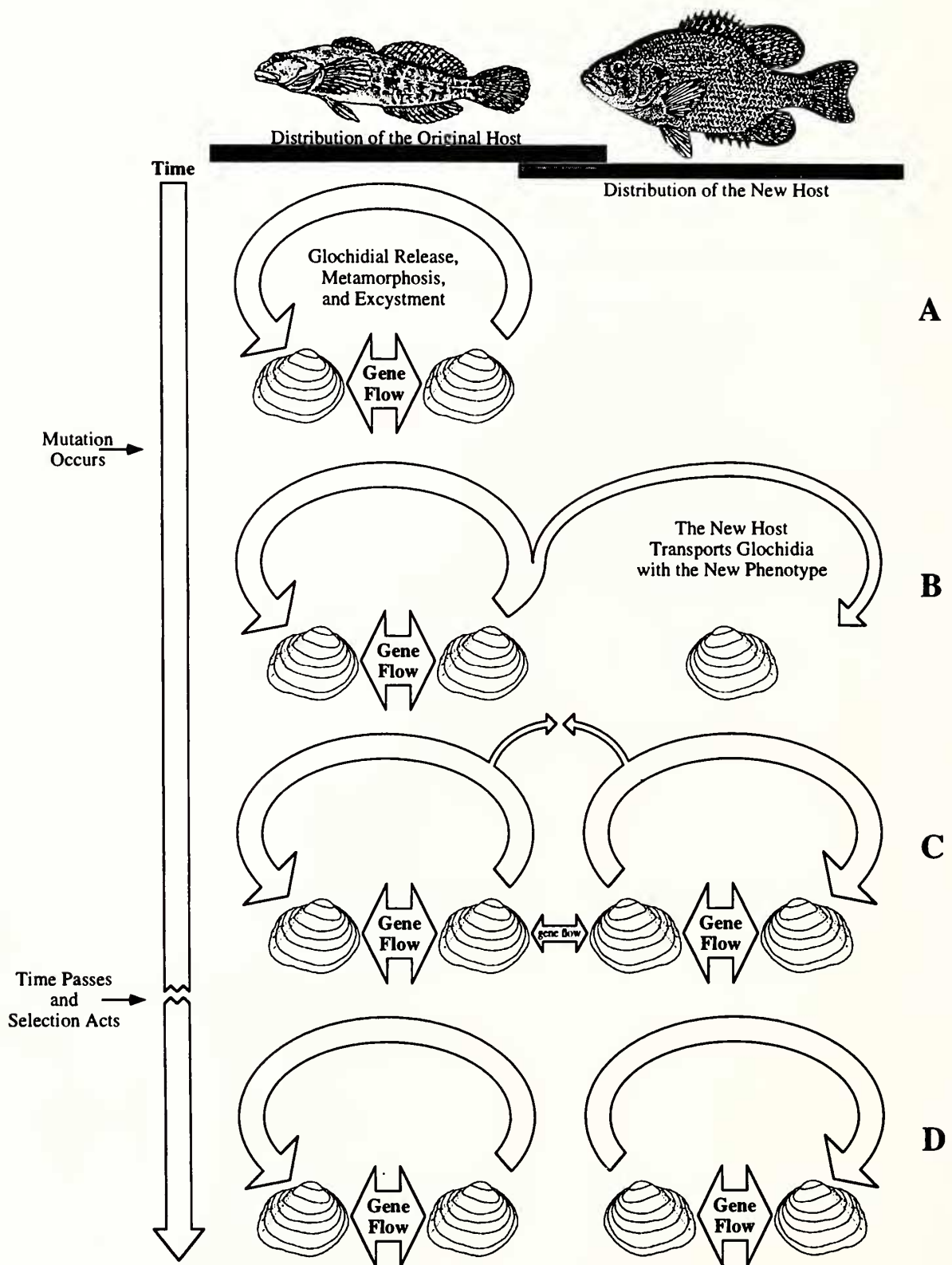
Fig. 1. Overview of the model of mussel speciation via host race formation. See text for discussion.

a distinct ecological difference between the two species, and I would predict that the fish host of *E. waccamawensis* is one of the endemic fishes of the Waccamaw drainage.

DISCUSSION AND CONCLUSIONS

Besides the two examples cited above, many other unionoidean taxa meet the criteria of this model for sympatric speciation via new host acquisition, including the limitation to one or a few host fish that share a common habitat preference. This appears contradictory to the widely held notion (*e. g.* Kat, 1984:199) that "... host specificity among unionaceans seems to be rather low." However, a critical examination of Hoggarth (1992) reveals that, of those associations confirmed by actual glochidial metamorphosis, greater than 73% of the 60 unionids reviewed are known to parasitize fish belonging to two or fewer genera. That is, for the parasite-host relationships thus far determined, the Unionoidea exhibit rather high fidelity to particular host genera. Within many of the host genera implicated, congeners share similar habitats and habits (K. Hartel, pers. comm.), and as it concerns the model, host specificity refers not so much to the number of species utilized but to the number of habitats frequented by those fishes.

The shortcoming of most models of ecological speciation is the difficulty of explaining how adapting to a new niche would lead to reproductive isolation. Under the assumption that the habitat preference of an organism could be changed by a mutation at a single locus, random interbreeding would tend to swamp the effects of the gradual accumulation of ecological separation between the two phenotypes (Mayr, 1947, 1970). The model presented here, however, is not based on the progressive acquisition of isolation. The fish hosts possess genetically hard-wired habitat preferences, and the mussels can capitalize on the niche fidelity fine-tuned during the evolution of the fish. Short effective fertilization distance completes the picture.

I do not argue that reproductive isolation via new host acquisition is a common mode of speciation in the Unionoidea. However, I would suggest that theories of speciation by geographical separation alone fail satisfactorily to explain the zoogeography and diversity of all mussel species in the Mississippi basin; the allopatric paradigm has yet to be corroborated by vicariance with the diversity of other families of aquatic organisms which would presumably reflect the same isolating events. Further, the habitat separation of genotypes achieved through the action of a shift in host fish could contribute to allopatric speciation following the erection of extrinsic barriers that subdivide populations (*e. g.* stream capture, etc.). Sympatric speciation via new host acquisition should be considered a viable alternative to allopatric speciation in the Unionoidea, and it

is a mechanism in need of further theoretical and experimental testing.

ACKNOWLEDGMENTS

LITERATURE CITED

Amyot, J.-P. and J. A. Downing. 1997. Seasonal variation in vertical and horizontal movement of the freshwater bivalve *Elliptio complanata* (Mollusca: Unionidae). *Freshwater Biology* 37:345-354.

Baker, F. C. 1928. The fresh-water Mollusca of Wisconsin. Part 2. Pelecypoda. Wisconsin Geological and Natural History Survey General Series 1301. *University of Wisconsin Bulletin* 70(2): 495 pp.

Bauer, G. and C. Vogel. 1987. The parasitic stage of the freshwater pearl mussel (*Margaritifera margaritifera* L.). 1. Host response to glochidiosis. *Archiv für Hydrobiologie* 76 (supplement):393-402.

Bush, G. L. 1974. The mechanism of sympatric host race formation in the true fruit flies (Tephritidae). *In: Genetic Analysis of Speciation in Insects*, M. J. D. White, ed. pp. 3-23. Australia and New Zealand Book Co., Sydney.

Coker, R. E., A. F. Shira, H. W. Clark, and A. D. Howard. 1921. Natural history and propagation of freshwater mussels. *Bulletin of the Bureau of Fisheries* 37:77-181. (Reprinted as Bureau of Fisheries Document No. 893.)

Davis, G. M., W. H. Heard, S. L. H. Fuller, and C. Hesterman. 1981. Molecular genetics and speciation in *Elliptio* and its relationships to other taxa of North American Unionidae (Bivalvia). *Biological Journal of the Linnean Society* 15:131-150.

Downing, J. A., Y. Rochon, and M. Pérusse. 1993. Spatial aggregation, body size, and reproductive success in the freshwater mussel *Elliptio complanata. Journal of the North American Benthological Society* 12:148-156.

Edgar, A. L. 1965. Observations on the sperm of the pelecypod *Anodontoides ferussacianus* (Lea). *Transactions of the American Microscopical Society* 84:228-230.

Fukuhara, S., M. Tabe, T. Kondo, and A. Kawamura. 1994. Difference in breeding season between two genetic types of *Anodonta woodiana* (Bivalvia: Unionidae) in a small creek. *Venus* 53:37-42.

Hoggarth, M. A. 1992. An examination of the glochidia-host relationships reported in the literature for North American species of Unionacea (Mollusca: Bivalvia). *Malacology Data Net* 3:1-30.

Isley, F. B. 1911. Preliminary note on the ecology of the early juvenile life

of the Unionidæ. *Biological Bulletin* 20:77-80.

Isley, F. B. 1914. Experimental study of the growth and migration of fresh-water mussels. Appendix III to the *Report of the U. S. Commissioner of Fisheries for 1913* (Reprinted as U.S. Bureau of Fisheries Document No. 792). 24 pp., 3 pls.

Johnson, R. I. 1970. The systematics and zoogeography of the Unionidae (Mollusca: Bivalvia) of the southern Atlantic Slope region. *Bulletin of the Museum of Comparative Zoology* 140:263-450.

Kat, P. W. 1983. Morphologic divergence, genetics, and speciation among *Lampsilis* (Bivalvia: Unionidae). *Journal of Molluscan Studies* 49:133-145.

Kat, P. W. 1984. Parasitism and the Unionacea (Bivalvia). *Biological Reviews* 59:189-207.

Kat, P. W. and G. M. Davis. 1984. Molecular genetics of peripheral populations of Nova Scotian Unionidae (Mollusca: Bivalvia). *Biological Journal of the Linnean Society* 22: 157-185.

Kraemer, L. R. 1970. The mantle flap in three species of *Lampsilis* (Pelecypoda: Unionidae). *Malacologia* 10:225-282.

Lefevre, G. and W. C. Curtis. 1910. Reproduction and parasitism in the Unionidae. *Journal of Experimental Zoology* 9:79-115, 5 pls.

Lynn, J. W. 1994. The ultrastructure of the sperm and motile spermatozeugmata released from the freshwater mussel *Anodonta grandis* (Mollusca: Bivalvia: Unionidae). *Canadian Journal of Zoology* 72:1452-1461.

Mathiak, H. A. 1979. *A River Survey of the Unionid Mussels of Wisconsin, 1973-1977.* Sand Shell Press, Horicon, Wisconsin. 75 pp.

Maynard Smith, J. 1966. Sympatric speciation. *American Naturalist* 100:637-650.

Mayr, E. 1947. Ecological factors in speciation. *Evolution* 1:263-288.

Mayr, E. 1970. *Populations, Species, and Evolution.* Belknap Press of Harvard University Press, Cambridge, Massachusetts. 453 pp.

Neves, R. J. and J. C. Widlak. 1988. Occurrence of glochidia in stream drift and on fishes of the upper North Fork Holston River, Virginia. *American Midland Naturalist* 119:111-120.

Ó Foighil, D. 1989. Role of spermatozeugmata in the spawning ecology of the brooding oyster *Ostrea edulis. Gamete Research* 24:219-228.

Ortmann, A. E. 1920. Correlation of shape and station in fresh-water mussels (Naiades). *Proceedings of the American Philosophical Society* 59:269-312.

Pennington, J. T. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. *Biological Bulletin* 169:417-430.

Strayer, D. L. 1981. Notes on the microhabitats of unionid mussels in some Michigan streams. *American Midland Naturalist* 106:411-415.

Strayer, D. L. and J. Ralley. 1993. Microhabitat use by some assemblages of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta. Journal of the North American Benthological Society* 12:247-258.

Tabe, M., S. Fukuhara, and Y. Nagata. 1994. Genetic difference between two types of swan mussel, in Japan. *Venus* 53:29-35.

Watters, G. T. 1994a. An annotated bibliography of the reproduction and propagation of the Unionoidea (primarily of North America). *Ohio Biological Survey Miscellaneous Contribution* No. 1. 158 pp.

Watters, G. T. 1994b. Form and function of unionoidean shell sculpture and shape (Bivalvia). *American Malacological Bulletin* 11:1-20.

Zale, A. V. and R. J. Neves. 1982. Fish hosts of four species of lampsiline mussels (Mollusca: Unionidae) in Big Moccasin Creek, Virginia. *Canadian Journal of Zoology* 60:2535-2542.

Ziuganov, V., A. Zotin, L. Nezlin, and V. Tretiakov. 1994. *The Freshwater Pearly Mussels and Their Relationships with Salmonid Fish.* Vniro Publishing House, Moscow. 104 pp.